

Anatomy of the “false thumb” of *Tremarctos ornatus* (Carnivora, Ursidae, Tremarctinae): phylogenetic and functional implications

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ABSTRACT

We describe for the first time the radial sesamoid or “false thumb” of the spectacled bear (*Tremarctos ornatus*), showing its great morphological similarities with that of the giant panda (*Ailuropoda melanoleuca*) and the differences with that of the rest of the Ursidae. This points to the existence of a common origin for this structure in both species, but considering the accepted phylogenies of ursids, the sharing of a “false thumb” in *T. ornatus* and *A. melanoleuca* would be a plesiomorphy for these groups, whereas in the rest of the ursids the radial sesamoid was probably reduced, lacking the specialised function that this bone has in Tremarctinae and Ailuropodinae.

Key words: Panda, radial sesamoid, Ursidae, Ailuridae, Anatomy, *Tremarctos*.

RESUMEN

Se describe por primera vez el sesamoideo radial o “falso pulgar” del oso de anteojos (*Tremarctos ornatus*), mostrando la gran similitud morfológica con el del panda gigante (*Ailuropoda melanoleuca*) y las diferencias que presenta con el resto de los Ursidae. Esto apunta a la existencia de un origen común para esta estructura en ambas especies, pero considerando las filogenias aceptadas de Ursidae, la presencia de falso pulgar en *T. ornatus* y *A. melanoleuca* sería una simplesiomorfía respecto al resto de úrsidos, en los cuales el sesamoideo radial nunca aumentó de tamaño, careciendo de la especializada función que posee en Tremarctinae y Ailuropodinae.

Palabras clave: Panda, sesamoideo radial, Ursidae, Ailuridae, Anatomía, *Tremarctos*.

Introduction

The family Ursidae FISCHER, 1817 includes large-sized carnivores, basically omnivorous and with a generalised postcranial skeleton (Ewer, 1973). Ursids are known from the Late Eocene, with *Cephalogale minor* (Ginsburg and Morales, 1995). There is no consensus about the phylogeny of the whole family, including fossil species, although following recent taxonomic classifications (MacKenna and Bell, 1997) we can consider 4 subfamilies within the family Ursidae: Tremarctinae (genus *Plionarctos* FRICK, 1926, *Pararctotherium* AMEGHINO, 1904, *Tremarctos* GERVAIS, 1855 and *Arctodus* LEIDY, 1854), Ailuropodinae (genus *Agriarctos* KRETZOI, 1942, *Ailuractos* QIU AND QI, 1989 and *Ailuropoda*

MILNE-EDWARDS, 1870), Ursinae (genus *Ursus* LINNAEUS, 1758, *Thalarctos* GRAY, 1825, *Helarctos* HORSFIELD, 1825 and *Melursus* MEYER, 1793) and Hemicyoninae (genus *Cephalogale* JOURDAN, 1862, *Agriotherium* WAGNER, 1837, *Hemicyon* LARTET, 1851, *Dinocyon* JOURDAN, 1861, *Zaragocyon* GINSBURG AND MORALES, 1995, *Phoberocyon* GINSBURG, 1955 and *Plithocyon* GINSBURG, 1955).

There are two extant species of carnivores known as “pandas”, the giant panda, *Ailuropoda melanoleuca* (DAVID, 1869) and the red panda, *Ailurus fulgens* CUVIER, 1825, traditionally joined under the same name owing to similarities in external appearance and diet, and the fact that both have developed a unique and highly specialised structure in the carpus, called “false thumb”. Nevertheless,

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there are no doubts about the fact that both carnivores belong to different families, Ursidae and Ailuridae (Goldman *et al.*, 1989; Ledje and Arnason, 1996; Bininda-Emonds *et al.*, 1999; Ginsburg, 1999; Flynn *et al.*, 1998, 2000, 2005), and the sharing of this structure is one of the most remarkable cases of evolutionary convergence among mammals (Salesa *et al.*, 2006). The “false thumb” is a small bone of the carpus, the radial sesamoid, which has enlarged, protruding posteriorly and thus acting partly as an opposable thumb: in association to the pisiform and when the fingers flex over the palm, it defines a pincer mechanism that allows the hand to manipulate food, basically bamboo branches (Endo *et al.*, 1999a; Roberts and Gittleman, 1984; Chorn and Hoffman, 1978). In general, sesamoid bones are small, more or less rounded masses embedded in certain tendons and usually related to joint surfaces, their functions being to modify pressure, to diminish friction, and occasionally to alter the direction of a muscle pull (Gray, 1977). The radial sesamoid of pandas lost these primary functions, becoming part of a pincer-like complex related to the manipulation of food. Nevertheless, although both panda species use this highly specialised structure for the same function, their different morphologies point towards a different phylogenetic origin (Salesa *et al.*, 2006, Antón *et al.*, 2006). Thus, the giant panda’s lineage would have developed the “false thumb” from terrestrial, bear-like ancestors, its primary function being the manipulation of food items, whereas in the red panda’s lineage (including some primitive forms with arboreal adaptations, such as *Simocyon batalleri* from the Late Miocene of Eurasia) the origin of this structure would be linked to the development of climbing capacities; in the more recent species of the red panda’s lineage, which developed a herbivorous diet, the “false thumb” adopted a secondary function in food manipulation, equivalent to that of *A. melanoleuca* (Salesa *et al.*, 2006).

The radial sesamoid is present in several species of Carnivora, but its size is comparable to that of other sesamoid bones, lacking the specialised function that this bone plays in pandas. Among extant ursids, only in the giant panda and the spectacled bear the radial sesamoid could be considered as non vestigial. Although in the polar bear (*Thalarctos maritimus*) its size is slightly larger than in other ursine bears, such as *Ursus arctos* (Endo *et al.*, 1999b), the size and morphology of this bone in all ursines are similar, that is, relatively small, rounded and compact.

The present paper describes for the first time the radial sesamoid of *Tremarctos ornatus*, showing that its morphology corresponds to the same pattern present in *Ailuropoda melanoleuca*. This implies that the hiperdevelopment of this bone is shared by both subfamilies Ailuropodinae and Tremarctinae, whereas Ursinae maintained the basic model seen in other Carnivora.

Material and methods

The material for anatomical comparisons belongs to the following institutions: complete specimen of male *Ailuropoda melanoleuca*, MNCN-12832, collections of comparative anatomy of the Museo Nacional de Ciencias Naturales-CSIC of Madrid (Spain); complete female specimen of *Tremarctos ornatus*, n.º 1661, Museo Anatómico of the Facultad de Medicina, Universidad de Valladolid (Spain); complete female specimen of *Ailurus fulgens*, n.º 2031, Museo Anatómico of the Facultad de Medicina, Universidad de Valladolid (Spain). The fossils of *Simocyon batalleri* from the locality of Batallones-1 (Torrejón de Velasco, Madrid) are housed in the collections of the Museo Nacional de Ciencias Naturales-CSIC of Madrid (Spain).

Anatomy of the Radial Sesamoid in Ursidae and Ailuridae

The radial sesamoid articulates to the posterior tubercle of the scapholunar by means of a smooth and sub-elliptic facet. The corresponding facet on the scapholunar shows a different development among the three studied species, in *A. melanoleuca* and *A. fulgens* being very marked, whereas in *T. ornatus* it is much less marked. Among the species with a well-developed radial sesamoid, there are two distinct morphologies (Salesa *et al.*, 2006): in the ailurids *S. batalleri* and *A. fulgens* the radial sesamoid is a cillindric, relatively small bone that displays a marked concavity in its distal tip (fig. 1), whereas in *A. melanoleuca* its size is relatively much larger, it is medio-laterally flattened and has a clearly hooked distal tip (fig. 2) (Antón *et al.*, 2006; Salesa *et al.*, 2006). The radial sesamoid of *T. ornatus* fits well in the latter morphology, which could be named as “ursid type”, although its size is much smaller than that of *A. melanoleuca*, its distal tip being just scarcely developed, remaining as a small and blunt protuberance (fig. 2). The two radial sesamoid morphologies would be thus reflecting the independent evolution of this structure in Ailuridae and Ursidae (Antón *et al.*, 2006; Salesa *et al.*, 2006). Concerning the relative size of this bone, only in *A. melanoleuca* it can

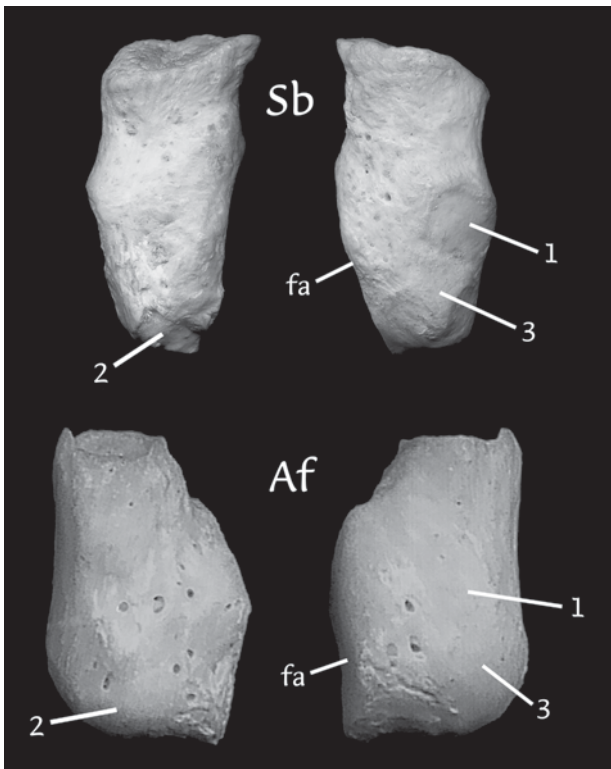


Fig. 1.—Left radial sesamoids of *Simocyon batalleri* (Sb) and *Ailuropoda fulgens* (Af) at the same size in medial (left) and lateral (right) views, showing the articular facet for scapholunar (fa) and the muscular attachments: 1) muscle *abductor pollicis brevis*; 2) muscle *abductor pollicis longus*; 3) muscle *opponens pollicis*.

be considered to be hiper-developed, reaching a similar size to that of the first metacarpal. In *A. fulgens*, *S. batalleri* and *T. ornatus*, this bone is just slightly larger than any other sesamoid of the carpus.

A complex of muscles related to the flexion and supination of the forearm attaches on the radial sesamoid, leaving a set of scars on this bone, of different development among the species. In *S. batalleri* the muscular attachment surfaces on the radial sesamoid are similarly developed as in *A. fulgens*, basically reflecting the same muscular pattern. The muscles *abductor pollicis brevis* and *opponens pollicis*, whose main function is to flex the thumb on the palm (Davis 1964; Gray, 1977) are short and thick in *A. melanoleuca* and *A. fulgens*, with their fibres so closely disposed that it is hard to distinguish two independent muscular masses (Davis, 1964; Antón *et al.*, 2006). These two muscles have a common origin in the antero-medial face of the radial sesamoid, attaching on the proximal tip of the first phalanx of the thumb, the attachment surface of the muscle

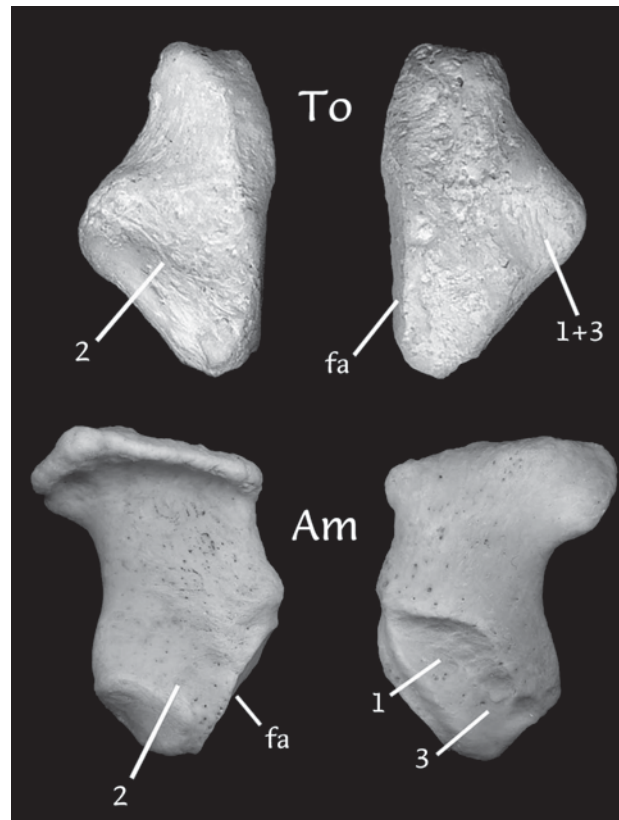


Fig. 2.—Left radial sesamoids of *Tremarctos ornatus* (To) and *Ailuropoda melanoleuca* (Am) at the same size in medial (left) and lateral (right) views, showing the articular facet for scapholunar (fa) and the muscular attachments: 1) muscle *abductor pollicis brevis*; 2) muscle *abductor pollicis longus*; 3) muscle *opponens pollicis*; 1+3, common attachment area of the muscles *abductor pollicis brevis* and *opponens pollicis*.

opponens pollicis being placed beneath that of the *abductor pollicis brevis*. In *A. melanoleuca*, these attachment surfaces are found along the proximal border of the radial sesamoid, in which an articulation facet for the scapholunar is developed, whereas in *S. batalleri* and *A. fulgens* these attachment surfaces are distally displaced. In *T. ornatus* both muscles *opponens pollicis* and *abductor pollicis brevis* are fused in a single muscular mass (Davis, 1964), and this is the reason why only one attachment surface can be distinguished on the radial sesamoid, relatively smaller than that of *A. melanoleuca*, and placed on the distal tip of the bone (fig. 2).

The muscle *abductor pollicis longus* originates on the lateral and posterior faces of radius and ulna, having in *A. fulgens* a double attachment on the postero-lateral face of the radial sesamoid and on the proximal border of the first metacarpal, by means of

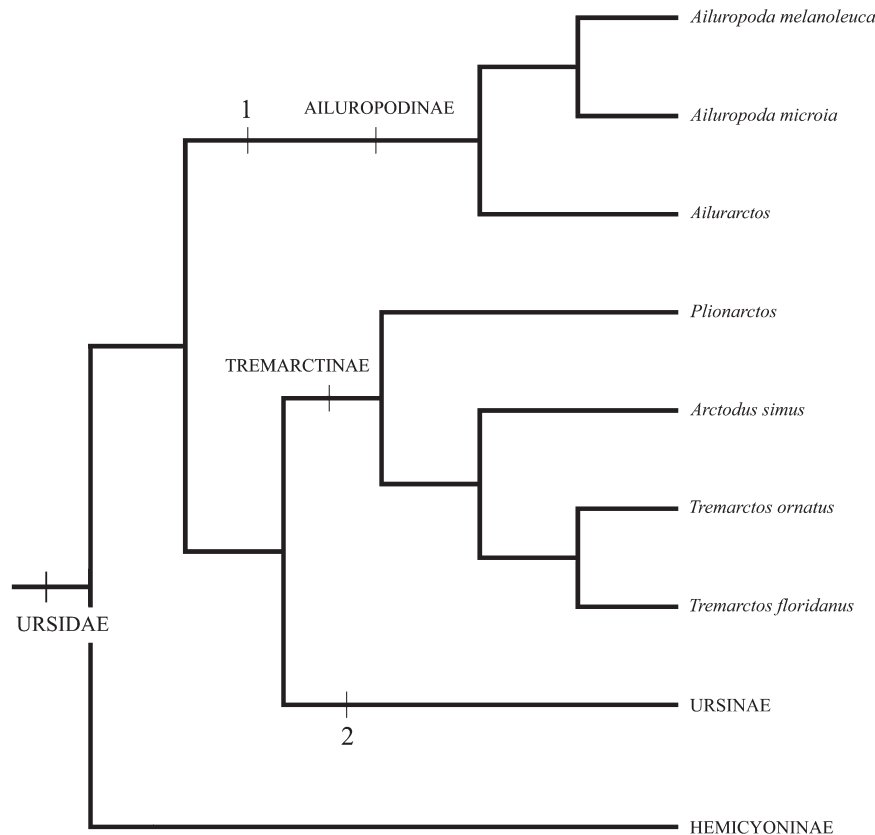


Fig. 3.—Cladogram of the family Ursidae based on those of Zhang and Ryder (1994), Talbot and Shields (1996), Waits *et al.* (1999) and Yu *et al.* (2004), showing the proposed hypothesis about the presence of “false thumb” in the Tremarctinae and Ailuropodinae: 1) hiperdevelopment of the “false thumb”; 2) reduction of the “false thumb”.

two tendons of similar thickness (Antón *et al.*, 2006). Davis (1964) cites the presence of this double attaching in *Ursus americanus* and *T. ornatus*, although emphasizing that the tendon on the first metacarpal is thicker than that on the radial sesamoid. In *A. melanoleuca*, the muscle attaches only on the radial sesamoid, lacking any attachment on the first metacarpal (Davis, 1964). The function of the muscle *abductor pollicis longus* is to contribute to the supination of the palm and flexing the thumb on the palm (Davis, 1964; Antón *et al.*, 2006).

Functional and Phylogenetic Implications of the Morphology of the Radial Sesamoid in *T. ornatus*

Among the Carnivora, the radial sesamoid has a similar size and shape than that of any other sesamoid (Davis, 1964); only Ailuridae, *A.*

melanoleuca and *T. ornatus* have enlarged their radial sesamoids, actually developing a different function from that of other sesamoids. In *A. fulgens* and *A. melanoleuca*, this “false thumb” is used during food manipulation, allowing the hand to hold bamboo branches whilst the animal pulls up the leaves (Davis, 1964; Roberts and Gittleman, 1984; Chorn and Hoffman, 1978). For *S. batalleri*, which shows a generalised dentition, lacking any trait of herbivorous adaptations, the presence of a “false thumb” has been interpreted as an aid in arboreal locomotion (Salesa *et al.*, 2006). The diet of *T. ornatus* is mostly herbivorous, based primarily on bromeliad hearts, berries, palm hearts and fleshy fruits (Brown, 1993; Welch *et al.*, 1997; Hilderbrand *et al.*, 1999; Ríos-Uzeda *et al.*, 2006) but there is no evidence on the use of the radial sesamoid in feeding activities. Given the size of this bone in *T. ornatus*, it is probable that its functionality is restricted, with this species having a

similar degree of dexterity in item manipulation as other ursid and arctoid carnivores such as *Procyon*, *Nasua* or *Bassariscus*. All these species, lacking an enlarged radial sesamoid, are capable of simple item manipulation, such as food washing or overturning stones (Davis, 1964; Lotze and Anderson, 1979; Gambaryan, 1974). Nevertheless, the kind of food manipulation seen in *T. ornatus* is more elaborated than those activities, since it consists in removing the leaves of bromeliads and palms to obtain the heart, which is less fibrous and easier to digest than the external parts (Paisley and Garsheles, 2006). This probably explains the higher degree of development of the radial sesamoid in this species in relation to other ursids, but it is also noticeable that *T. ornatus* being the most arboreal among bears (Peyton, 1999; Ríos-Uzeda *et al.*, 2006), the presence of an enlarged radial sesamoid could also help in arboreal locomotion, as has been interpreted for *S. batalleri* (Antón *et al.*, 2006; Salesa *et al.*, 2006). Thus, the model of "false thumb" seen in *T. ornatus* would be morphologically very close to that of the common ursoid ancestor (fig. 3), which would have a radial sesamoid very similar to that of this species. Thus, the presence of a "false thumb" in *T. ornatus* would be a primitive character shared with other fossil ursids such as *Arctodus simus*, from the Pleistocene of North America, and *Tremarctos floridanus*, from the Pleistocene and Holocene of North America (Kurtén, 1966), as shown by the presence of a marked facet for this bone in the scapholunar. The herbivorous diet and the arboreal capacities of *T. ornatus* are probably retentions of the primitive model, whereas the cursorial adaptations of *A. simus* (Kurtén, 1967; Matheus, 1997) would be an autapomorphy for this species.

The presence in Tremarctinae of an apparently specialised structure such as the "false thumb", shared with Ailuropodinae, should be considered as a simplesiomorphy, rather than as a sinapomorphy of Tremarctinae+Ailuropodinae. Although only the latter has hiperdeveloped the radial sesamoid, providing it with a new function in food manipulation, the Tremarctinae probably started the same path, although without significant changes in the size of this bone relative to the primitive model. It is tempting to link Tremarctinae + Ailuropodinae in base of this shared feature, but the more recent molecular phylogenies of ursids (fig. 3) agree in supporting the clade Tremarctinae + Ursinae. Following this, it is more likely that in Ursinae the

radial sesamoid suffered a process of reduction from an ancestor with a slightly flattened but still not enlarged bone. Thus, the morphology of the radial sesamoid of these primitive ursids is revealed as an important character to trace the origin of the modern groups within the family Ursidae, and only future findings of this bone in fossil species will contribute to elucidate its complete evolutionary history.

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